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BIOLOGY OF THE HALF-WING GEOMETER, *PHIGALIA TITEA* CRAMER (GEOMETRIDAE), AS A MEMBER OF A LOOPER COMPLEX IN WEST VIRGINIA[1]

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ABSTRACT. Field and laboratory studies were conducted during 1983 in two counties of eastern West Virginia where forest defoliation by a looper complex (Geometridae) had been heavy the previous two years. *Phigalia titea* Cramer, dominated, making up 77–94% of feeding larvae; *Erannis tiliaria* (Harris), *P. strigateria* (Minot) and *Alsophila pometaria* (Harris) were also present. Adult *P. titea* were found in the field from 17 March to 26 April, eggs from 17 March to 3 May and larvae from 3 May to 15 June. Descriptions of oviposition sites and eggs are given; females were found to contain a maximum of 1447 eggs. At constant 24°C *P. titea* larvae required a mean total of 28 days to mature through five instars when fed on sugar maple leaves, but larval growth rates were found to vary with host plant species. Descriptions of the five larval instars are given.

As defoliators of hardwood forests numerous species of native geometrids produce either consistent but little noticed damage or sporadic but significant damage during outbreaks in eastern hardwood forests. Outbreaks may consist primarily of a single species or represent a complex of geometrid defoliators.

During the spring of 1981 and 1982, approximately one million acres of hardwoods in eastern West Virginia were defoliated each year to varying degrees ranging from 20–100%. The West Virginia Department of Agriculture assessed the looper infestation as causing more damage to hardwoods in one year than all other defoliators in the state have in the past 20 years. Loopers have been the most obviously destructive forest insects in West Virginia in recent times, with numerous reports of tree mortality following heavy defoliation (Anon., 1983). While various species were suggested as comprising the defoliator complex, no detailed observations had been made (Anon., 1981, 1982).

The extensive defoliated acreage and resulting mortality of hardwoods, especially oaks and hickories, justified a more detailed study on the looper complex in West Virginia. Sampling of larval populations showed four looper species to be present at all study sites: *Phigalia titea* Cramer, *P. strigateria* (Minot), *Erannis tiliaria* (Harris) and *Alsophila pometaria* (Harris). In all samples *P. titea* made up the majority of the looper population, ranging from 77% to 94%, depending on the site. While some information on *P. titea* is available (Baker,

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1972; Talerico, 1968), it is often of a superficial nature or contains information contrary to observations made during this study. The outstanding exception is the fine study of adults by Rindge (1975).

METHODS AND MATERIALS

Study Area

Three sampling sites were selected in West Virginia. Two were in Cacapon State Park in Morgan County of West Virginia's Eastern Panhandle within the most heavily defoliated region; the third site was near Elkhorn Mountain at the border of Grant and Hardy counties on the southern edge of the affected region. The vegetation at all sites is often referred to as oak-hickory-pine, although originally chestnut was a dominant species. Both study areas are dry upland sites consisting in part of steep shale slopes.

The two Cacapon State Park sites were on Cacapon Mountain. The site designated Batt Picnic Area (Batt PA) was east facing at an elevation of 381 m and had complete looper defoliation in 1982. The second site, designated Cacapon Overlook (Cac. OL) was along both sides of a north/south ridge at an elevation of 701 m and suffered about 25% looper defoliation in 1982. The Elkhorn (Elk.) study area was on Getz Mountain, 1–2 km south of Elkhorn Mountain, at an elevation of about 732 m. During 1982 the Elkhorn area also received about 25% looper damage.

Field Collection and Description of Looper Life Stages

Sampling for all looper species was initiated with adult observations on 17 March 1983 at Cacapon State Park and 24 March at Elkhorn Mountain. Samples were taken at 6- to 8-day intervals through 15 June, at which time most larvae had moved into the soil for pupation.

During the weeks of adult *Phigalia* activity, collections were made and relative numbers and locations of males and females were noted during timed walks through each study site. Males were determined to species through genitalia dissection; females were collected for determination of species and fecundity. Fecundity was studied by two methods: (1) dissection of field collected females and (2) caging of females on dead twigs for oviposition, counting deposited eggs and then dissecting the post-ovipositional females to count residual eggs.

Phigalia eggs were observed in the field and developmental color changes noted on a weekly basis. Eggs on dead twigs or other vegetation were collected from 17 March through 26 April, were held 1 to 4 weeks at 4°C, then placed at room temperature to hatch; viability was determined.

TABLE 1. Potential egg counts from dissected female *Phigalia titea* collected at various dates and study sites in 1983. Sample size given in parentheses.

Site	Date	No. eggs/female	Range
Batt PA	III.17 (40)	309	21–884
	III.24 (5)	215	11–454
	IV.7 (7)	48	9–114
	IV.14 (7)	23	8–51
	IV.20 (5)	29	7–54
Cacapon OL	III.24 (1)	1364	
	III.31 (6)	542	395–836
	IV.14 (6)	859	288–1409
Elkhorn	III.24 (2)	910	643–1177
	III.31 (6)	775	177–1447

At each sampling date between larval hatch and pupation, foliage samples were collected with pole pruners and placed in plastic bags for transport to the laboratory. Samples of 100 to 200 larvae were taken from the pruned vegetation and preserved for determination of species, and in the case of *P. titea*, to determine instar composition and to prepare larval descriptions.

Larval Development

To determine intervals between larval molts, newly hatched larvae from the egg viability study were placed in groups of 10 on leaf clusters of host plants in petri dishes and held at 24°C. In one experiment, 200 first instar larvae were reared on sugar maple; one group of 100 set up 27 April, a group of 20 set up 6 May and a group of 80 set up 11 May. In a second experiment begun 4 May, growth rates of larvae were compared when fed on red oak and red maple; 50 larvae were reared on each food plant.

RESULTS AND DISCUSSION

Fecundity

Most of the *P. titea* females collected from Batt PA for dissection were already ovipositing, and the resultant potential egg count may have been lower than the number of eggs which they were capable of producing. The expected trend of lower potential egg numbers per female with increasing time into the season is shown in Table 1. Females collected at Batt PA from 7 to 20 April were depleted.

Egg counts of dissected females from Cac. OL and Elk. were considerably higher than oviposition rates previously reported for *P. titea*; Talerico (1968) reported that several caged females produced from

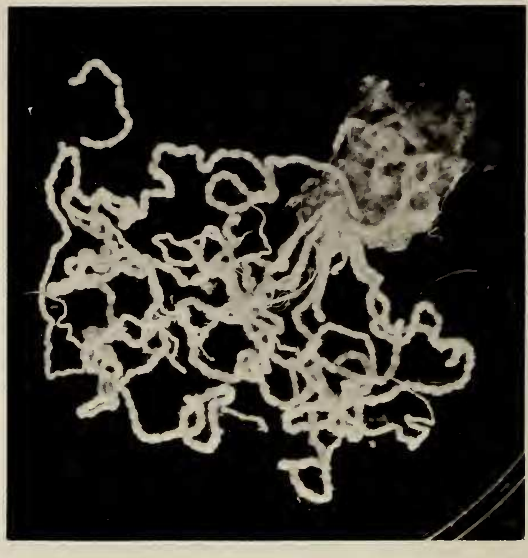

FIG. 1. Dissected ovaries of a *Phigalia titea* containing 1364 eggs.

127 to 139 eggs each. Data show that dissection of preovipositional females gives an accurate indication of reproductive potential since 90% of eggs were laid in the laboratory cages (Table 2). The highest egg count from a dissected female was 1447. Figure 1 shows dissected ovaries of a *P. titea* female with 1364 eggs. The four ovarioles per ovary contained the following egg numbers: 166, 164, 193, 157, 184, 185, 153, 162.

Oviposition Sites and Egg Descriptions

Eggs were generally laid on dead twigs, singly or in clusters, with the cluster configuration and size depending upon structural features of the oviposition site. Common oviposition locations were under loose, flaking bark of dead twigs of maples (*Acer* spp.), oaks (*Quercus* spp.), black gum (*Nyssa sylvatica* Marsh.), common witch hazel (*Hamamelis virginiana* L.), flowering dogwood (*Cornus florida* L.), grape (*Vitis* spp.) and around bark cracks of hickory (*Carya* spp.) twigs. Many clusters were under loose bark at crotches of dead twigs. Other locations included deep splits in dead twigs, bostrichid burrows, frass of shallow buprestid or cerambycid burrows, exposed face of girdled twigs, empty chorions of Saturniidae, small Lepidoptera pupae or cocoons, spider egg sacs, and dead crumpled leaves of composites from the previous year. One of the most interesting locations was inside empty chorions of previous year's eastern tent caterpillar, *Malacosoma ameri-*

TABLE 2. Egg counts for female *Phigalia titea* allowed to oviposit in the laboratory and subsequently dissected. Sample size given in parentheses.

Site	Date	# eggs laid		# eggs/dissected female		Mean total/ female	Range
		Mean	Range	Mean	Range		
Cacapon OL	IV.7 (8)	724	496–1035	65	3–243	789	551–1266
	IV.14 (3)	686	242–1022	26	11–49	712	260–1133
	IV.20 (5)	664	280–1128	40	3–123	704	299–1251
Elkhorn	IV.7 (5)	394	72–545	36	7–83	430	155–597
	IV.14 (9)	601	41–1140	49	2–278	650	60–1198
	IV.26 (5)	337	110–432	53	5–147	390	115–516

canum (Fab.), egg clusters (J. E. Weaver, pers. observ.). Diameters of 65 randomly collected egg-bearing twigs of various host species averaged 7.2 mm (range 2–15 mm) at the oviposition sites.

Eggs were slightly roughened by reticulate sculpturing, as previously described by Forbes (1948). The shape was oval with one end of the egg more flattened or broadly rounded and the opposite end more conical; heaviest sculpturing was at the broad end. Measurement of 80 eggs collected at both sites at Cacapon State Park on various dates averaged 0.905 (0.858–0.990) mm long and 0.521 (0.495–0.561) mm wide: These sizes were only about half that reported for *P. titea* eggs in Virginia (Talerico, 1968).

When first deposited, eggs were greenish yellow to yellow in contrast to an earlier description by Talerico (1968). Further color changes reflected embryonic development, the rate of which is temperature dependent. Within 2 to 3 days at 24°C, eggs began developing a salmon pink color which first appeared at the blunt end of the egg. The eggs gradually became darker pink over a period of several days, and when approaching maturation, dark red to black spots appeared at the blunt end. At about 24 h prior to hatch, the eggs appeared dark purple as a result of the dark head capsule and body of the larva being visible through the lavender chorion. At this stage, microscopically, the larva was seen curled inside with head and posterior end meeting at the blunt end of the egg. The pale spiracular stripe of the larva was easily seen. At constant 24°C, development time from oviposition to hatch required 7 to 8 days.

Larvae eclosed by chewing an irregular hole through the blunt end of the egg. Empty chorions were an iridescent lavender and were easily observed in the field. Eggs parasitized by *Telenomus alsophilae* Viereck (Hymenoptera: Scelionidae) appeared chocolate brown at the time adjacent unparasitized eggs were hatching. In the laboratory, parasite adults did not eclose until about 13 to 15 days after *P. titea*

TABLE 3. Comparison of developmental time for *Phigalia titea* larvae reared on sugar maple,[a] red oak[b] and red maple.[b]

	Time in instar (days)					
	Mean			Range		
Instar	Sugar maple	Red oak	Red maple	Sugar maple	Red oak	Red maple
1	4.30	4.24	4.50	3–5	3–5	3–5
2	3.02	3.18	3.18	2–5	2–4	2–4
3	3.50	2.74	3.70	2–5	2–4	2–5
4	3.43	3.36	4.30	2–6	2–4	3–6
5	7.66	6.92	7.24	6–11	6–8	6–9
Prepupa	6.90	5.88	7.06	4–10	5–7	6–9
Total	28.41	26.32	29.98	21–40	20–31	24–36

[a] Based on 200 larvae.
[b] Based on 50 larvae.

larval hatch. Chorions of parasitized eggs retained a brown color, thus allowing easy evaluation of percent parasitism in a field situation.

Percent hatch of 12,855 eggs randomly collected at the three study sites averaged 94.4. Some eggs which failed to hatch had obviously suffered mechanical injury at collection; many eggs remained dark yellow as if no embryonic development had occurred, while others were dark pink. Dead larvae were observed in some eggs. Parasitism was low in all egg collections and, at most sites, did not appear to contribute significantly to mortality.

Larval Growth Rates

As reported by Talerico (1968) and confirmed in this study, *P. titea* has five larval instars. Growth data for 200 larvae reared from eggs which hatched on three different dates are combined and given in Table 3. It was obvious from this evaluation that time spent per instar was related to developmental stage of host plant foliage. Larvae which hatched on 27 April were reared on the flowers and very young leaves of sugar maple, larvae from 6 May on young to moderately aged leaves and larvae from 11 May primarily on mature leaves. Greater length of time was required between 1st instar and prepupation with increasingly older foliage, e.g. larvae set up on 27 April matured on the average 6 days faster than larvae set up on 11 May. This difference is not apparent in Table 3, however, since all data are combined.

As expected, larvae reared on different host plants develop at different rates. The period from hatch to pupation was about 26 days for red oak and about 30 days for red maple. Field observations during the 1983 season substantiated this finding. At any point during the larval season, later instar larvae were always on oak, hickory and birch and earlier instars on dogwood, maple, blackgum, witch hazel, and most other hosts.

Larval Description

Talerico (1968) made only brief reference to larval color patterns. Descriptions of color patterns of each instar from the populations within the West Virginia study areas are given below. Head capsule widths are the average of 50 specimens per instar.

Instar 1. Head capsule (0.329 mm) medium to dark reddish brown with paler frons. Ground color of body of newly hatched larvae slate grayish black. Dorsal pinnaculae dark, dull yellow; pair of small pale yellow middorsal pyramidal streaks at posterior margin of each segment from mesothorax through abdominal segment 6. Spiracular stripe from creamy white to pale yellow, extending almost continuously from prothorax through abdominal segment 6. Subspiracular area brownish to yellowish brown. Caudal shield and anal prolegs medium brown to dull yellow-brown. Late 1st instar larvae appear much more pale, with medium olive ground color, after intersegmental areas are exposed with larval growth. Particularly prominent just prior to molt is dull yellow-brown cervical area which is protuberant and dwarfs head capsule. In mature 1st instars, caudal, cervical, and proleg sclerites medium brown and very evident against paler body.

Instar 2. Head capsule (0.621 mm) dark reddish brown to black with pale maculations. Basic body ground color greenish brown to slate black. Paired cervical shields small but prominent. Pair of fine, indistinct white dosal stripes down length of body but discontinuous between segments. Pinnaculae dark. Spiracular stripe diffuse and faint, but present; fades out on abdominal segment 7. Secondary setae present but sparse on body, located primarily above spiracular line.

Instar 3. This is the first instar that begins to develop a striping pattern approaching that of mature larvae. These larvae, however, are very dark; mature individuals appear shiny black, with striping being evident only under magnification.

Head capsule (1.05 mm) black with prominent grayish white mottled areas. Fine irregular grayish white striations down length of body. Paired dorsal stripes filled with small orange spots on posterior margin of each segment. Pinnaculae black. Diffuse orange coloration along spiracular area most prominent on protuberances of abdominal segments 1 and 5; lateral orange areas of thoracic segments and abdominal segment 6 reduced. Caudal and cervical areas black with white mottling; venter black. Secondary setae more numerous than in previous instar including some below spiracular line.

Instar 4. Head capsule (1.87 mm) black and white mottled with a higher proportion of white than in previous instar. Frons mottled, clypeus white. Two pairs of black irregular dorsal stripes, orange-filled. Supraspiracular stripe a pair of black irregular lines, white-filled and flanked with orange. Spiracular area with pair of black irregular lines, white-filled, running just above and below spiracle. Area in immediate vicinity of spiracle on each segment prominently suffused with orange. Setae SD1, L1 and L2 within this orange area and each on separate black chalaza. Spiracular chalazae of second abdominal segment most prominent; abdominal segment 8 with pair of prominent chalazae forming dorsal hump. Subspiracular stripe of double irregular black lines, grayish-white-filled. Shields mottled black and white. Legs black; abdominal sternites 7 to 8 white.

Instar 5. Head capsule (2.83 mm) white with distinct black maculations. Body ground color pale lavender-gray with pairs of fine irregular black lines, orange-filled dorsally, pale gray-filled subdorsally. Orange patterns, chalazae, shields and venter as in instar 4. Peritremes black; spiracular valve off-white. Basic appearance of this larva paler with striping more prominent than in previous instars.

P. titea Pupae

The pupa of *P. titea* is illustrated by Talerico (1968). During the current study, measurements were made of 80 pupae; mean length was 13.45 mm and range was 11–15.5 mm. Length was not related to sex, but female pupae were characteristically stouter.

Life History

Adult *P. titea* emerged from the soil where they overwintered as pupae and climbed vertical surfaces. Males eclosed several days to a week before females and were most commonly seen resting on tree trunks. Females climbed tree trunks of a wide range of sizes and remained there for a period of hours to a day or two. Females (and thus eggs) were rarely found on small dead trees. Mating most commonly occurred on tree trunks, after which females climbed upward to locate suitable oviposition sites.

Male *P. titea* were first observed flying at Berkeley Springs, WV, near Cacapon State Park on 8 March. At Batt PA on 17 March, males were numerous and resting on tree trunks. The total numbers of females appeared relatively less than males, because of their virtual winglessness and related cryptic appearance and, because their behavior rendered them more difficult to observe; 40 females were found in a 2 h walk. Most of the Batt PA females were on dead twigs, but some were still emerging from the soil and beginning to climb tree trunks. Of the few eggs present on the twigs, about 99% were yellow. The number of adults seen on 24 March was similar to that of the previous week; numbers of observed females and males began to decline by 31 March and continued to decline markedly each week. The last male was observed at Batt PA on 14 April and the last female on 26 April.

A few males were seen at Cac. OL on 17 March and at Elk. on 24 March. Females were observed for the first time on the latter date at both sites. Numbers of adults continued to increase at Cac. OL and Elk. through 7 April, then sightings began to decline on 14 April. No males and low numbers of females were seen on 26 April. Adult populations of *P. titea* were markedly lower at Cac. OL and Elk. than at Batt PA. At peak female activity, an average of 8 to 10 were observed in a 2 h walk.

A few eggs were seen at Batt PA on 17 March with more than 99% of these being yellow. The first ovipositing females were observed at Elk. on 24 March and at Cac. OL on 7 April. By the later date, about 10% of eggs at Batt PA were pink and females at Elk. and Cac. OL were reaching peak oviposition activity. On 14 April, about 90% of the eggs at Batt PA were pink, while at other sites only about 20% had developed pink coloration. By 26 April, 95% of the eggs at Cac. OL and Elk. were pink.

Egg hatch began in early May and by 3 May was about 85% complete at Batt PA; remaining eggs were in the purple stage, indicating hatch would occur within about 24 h. At Batt PA, 1st instar larvae were very evident, as they hung on silk lines below the dead twigs on

TABLE 4. Instar composition (% of population) of *Phigalia titea* taken at study sites between 3 May and 8 June.

Date	Instar	Study site Batt PA	Cacapon OL	Elkhorn
V.3	1	87	90	100
	2	13	10	
V.10	1	6	73	94
	2	87	26	6
	3	7	1	
V.17	1	0	40	0
	2	4	52	82
	3	59	7	17
	4	37	1	1
V.24	2	0	13	3
	3	2	67	71
	4	28	19	26
	5	70	1	0
V.31	3	0	4	3
	4	2	78	52
	5	98	18	45
VI.8	4		8	7
	5		92	93

which eggs had been laid. Ballooning actively occurred, with the larvae riding air currents into trees which were just beginning to leaf. It appeared that larvae arrived at potential host trees randomly by means of wind activity, but they showed preference for hosts by either settling quickly and beginning to feed or continuing to balloon if the initial host was not suitable. Considerable larval mortality probably occurred at this time.

On 3 May at Batt PA, some larvae were beginning to feed with damage being initially in the form of pinholes and skeletonizing. On this date at Cac. OL, egg hatch was about 20% complete but was just beginning at Elk. No feeding was evident at these sites.

Despite the fact that eggs were laid over a period of several weeks at each site, egg hatch at any one site occurred relatively in synchrony due to effect of low temperatures on earlier laid eggs. Progression of *P. titea* larval development for each of the study sites is given in Table 4. Differences in altitude and temperature at the study sites produced developmental events, resulting in adult emergence to pupation being one to two weeks earlier at Batt PA than at the other two sites. Differences in developmental time also occurs depending on orientation of slope.

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